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PLANT-ANIMAL INTERACTIONS - ORIGINAL PAPER

# Leaf miner and plant galler species richness on *Acacia*: relative importance of plant traits and climate

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**Abstract** Diversity patterns of herbivores have been related to climate, host plant traits, host plant distribution and evolutionary relationships individually. However, few studies have assessed the relative contributions of a range of variables to explain these diversity patterns across large geographical and host plant species gradients. Here we assess the relative influence that climate and host plant traits have on endophagous species (leaf miners and plant gallers) diversity across a suite of host species from a genus that is widely distributed and morphologically variable. Forty-six species of *Acacia* were sampled to encapsulate the diversity of species across four taxonomic sections and a range of habitats along a 950 km climatic gradient: from subtropical forest habitats to semi-arid habitats. Plant traits, climatic variables, leaf miner and plant galler diversity were all quantified on each plant species. In total, 97 leaf mining species and 84 plant galling species were recorded from all host plants. Factors that best explained leaf miner richness across the climatic gradient (using AIC model selection) included specific leaf area (SLA), foliage thickness and mean annual rainfall. The factor that best explained plant galler richness across the climatic gradient was C:N ratio. In terms of the influence of plant and climatic traits on species composition, leaf miner assemblages were best explained by SLA, foliage thickness, mean minimum temperature and mean annual rainfall, whilst plant gall assemblages were explained by C:N ratio, %P, foliage thickness, mean minimum temperature and mean annual rainfall. This work is the first to assess diversity and structure across a broad environmental gradient and a wide range of potential key climatic and plant trait determinants simultaneously. Such methods provide key insights into endophage diversity and provide a solid basis for assessing their responses to a changing climate.

**Keywords** Environmental gradient · Climate change · Endophagous insects · Community structure

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## Introduction

Hypotheses that have been put forward to explain endophagous herbivore species richness have provided variable results. Hygrothermal stress could explain the observations that leaf miner richness generally increases in mesic habitats and galler richness increases towards more arid habitats (Fernandes et al. 2004; Fernandes and Price 1992). Leaf miner and plant galler species richness and composition patterns could also be related to plant species richness and composition, geographic range of the host plants and soil nutrients (Blanche and Ludwig 2001; Blanche and Westoby 1995; Espirito-Santo and Fernandes 2007; Hespenheide 1991; Veldtman and McGeoch 2003). Species richness patterns could also be

related to the host plant chemical and physical traits that are unique to each taxon in particular climatic regions. However, it is clear that a range of climatic and plant traits will influence the diversity of different taxa across large geographical gradients. To date there has been no assessment of the relative influence that climate and host plant traits have on endophagous diversity across a suite of widely distributed and morphologically variable host species. Here we examine such patterns and their possible drivers for both leaf miner and plant galler assemblages within the genus *Acacia* in Australia.

Climatic conditions have long been linked to distribution patterns of a diverse array of taxa, and this is apparent from the species richness trends observed with latitude and altitude (Carneiro et al. 2005; Fernandes and Price 1988, 1991; Mittelbach et al. 2007; Price 1991). However, this trend is not consistent across all taxa, especially when equivalent habitats are assessed using comparable methods across the latitudinal range of a single host plant for species richness, herbivory and abundance–biomass relationships (Andrew and Hughes 2004, 2005b, 2008). Galling species represent an anomaly to the global trend, with studies documenting a peak in diversity at intermediate latitudes in environments of increasing temperature and aridity (Blanche and Ludwig 2001; Carneiro et al. 2005; Fuentes-Contreras et al. 1999; Goncalves-Alvim and Fernandes 2001). Increasing gall species richness in habitats that become hotter and drier has led to the hypothesis that the gall-forming habit is an adaptation to harsh or stressful environments (Baust et al. 1979; Carneiro et al. 2005; Crespi et al. 1997; Fernandes et al. 2004; Fernandes and Price 1988, 1991, 1992; Lara et al. 2002; Marques et al. 2000; Waring 1986). The gall itself appears to act as an effective protection against the direct action of climate, reducing levels of desiccation for the inducing insect (Baust et al. 1979; Carneiro et al. 2005). The observed higher levels of galling richness in xeric versus mesic sites is supported by differential success and mortality factors between climatic zones (Lara et al. 2002). Gallers that colonise plants in xeric sites have been found to be generally more successful, surviving to adulthood, than those that colonise plants in mesic sites (Fernandes and Price 1991, 1992). Lower rates of parasitism and fungal attack in xeric sites could explain the differential success between habitats (Blanche and Ludwig 2001; Carneiro et al. 2005; Fernandes et al. 2004; Fernandes and Price 1991, 1992; Goncalves-Alvim and Fernandes 2001). Galls in moist habitats also take longer to mature and harden (Fernandes and Price 1992), which could leave them more vulnerable to predators, disease and fungal attack in tropical climates. Climate-related leaf abscission could be a further factor influencing the richness of galler communities. Favourable habitats, in the tropical and temperate zones, generally have high levels of leaf abscission (Coley et al. 1985), with premature leaf abscission known to reduce insect fitness and cause mortality (Faeth et al. 1981a). High levels of leaf abscission may therefore limit populations of leaf- and petiole-galling insects in otherwise climatically favourable habitats. Despite support for a relationship between galler diversity and climatic conditions, i.e. gall maker species richness increases as environments become hotter and drier, contradictory evidence again provides some doubt that climatic factors have any effect (Blanche 2000).

Insect leaf-mining communities have higher species richness in more moist environments, which may be attributed to more suitable leaf types compared to more arid ones (softer larger leaves compared to thicker more sclerophyllous leaves) (Andrew and Hughes 2005b; Fernandes et al. 2004; Sinclair and Hughes 2008). Also leaf mines do not protect the resident insect from desiccation in hot, arid habitats, since leaf miners excavate just below the lamina, leaving only a thin layer of cells to cover the inhabitant (Connor and Taverner 1997). Climate also affects the richness of leaf mining communities through its direct impacts on plant traits (Connor et al. 1994), and overall host species distribution (Hnatiuk and Maslin 1988). For example, leaf thickness may be strongly influenced by climatic factors, with harsher habitats showing increased thickness, especially in *Acacia* (Cunningham et al. 1999). This impacts on mining richness, as adults preferentially select the thinnest, largest leaves for oviposition (Faeth et al. 1981b; Sinclair and Hughes 2008). Aside from the well-noted impact of desiccation in the determination of mining insect distributions, a number of other elements have also been considered. The increase in mining richness observed in the tropics may also be linked to increased leaf water content and relative humidity. Low leaf water has been associated with reduced growth rates, which has obvious impacts on overall fitness (Scriber 1977). Low relative humidity also appears to decrease growth rate and may affect general pupal weight (Scriber 1977). These impacts on individual fitness may have flow on effects on total populations, limiting miner richness in arid areas.

By focusing on a suite of host species within a genus of widely distributed and morphologically variable taxa, we are able to examine the relative contributions that host plant traits and climate make towards explaining endophagous diversity. Here we assess leaf miner and plant galler assemblages across an aridity gradient in the genus *Acacia* (subgenus *Phyllodineae*) within Australia. We assess the relative influence of host plant traits and climate on endophagous diversity and pose the following question: what is the relationship between climatic and plant physical

traits and gall maker and leaf miner (1) species richness and (2) assemblage structure?

## Methods

### Study host plants

*Acacia* is the largest plant genus in Australia, with more than 950 species currently recognised (Maslin 2004; Morris et al. 2002). Following Maslin (2004), the genus *Acacia* is separated into three subgenera: *Acacia*, *Aculeiferum*, and *Phyllodineae*. The subgenera *Acacia* and *Aculeiferum* contribute fewer than ten species to Australia's flora and are principally confined to the north of the continent. Taxa from the subgenus *Phyllodineae* are most dominant, and are divided into seven sections (Pedley 1978): *Phyllodineae*, *Juliflorae*, *Plurinerves*, *Botrycephalae*, *Alatae*, *Lycopodiifolae*, and *Pulchellae*. They exhibit variations in foliage type (adult bipinnate true leaves, or phyllodes that are modified leaf petioles), size, shape, plus venation and inflorescence form (Miller and Bayer 2001). The sections *Phyllodineae*, *Juliflorae*, *Plurinerves*, and *Botrycephalae*, which account for most taxa of the subgenus *Phyllodineae*, are well represented in eastern Australia and exhibit a range of foliage traits.

Forty-six species of *Acacia* were sampled from 18 sites across a 950 km transect (Fig. 1), representing a gradient of decreasing annual rainfall across them (Table 1). Sites were selected based on host plant species having populations of greater than 40 individuals at any one site. All sampling was conducted between September 2007 and March 2008. The 46 plant species were selected to represent the four dominant Australian sections of the subgenus, and their sample locality was spread across the gradient. Each plant species was only sampled at one location to preserve independence of samples, even if a host plant species was found at multiple sites along the gradient. Effectively each host plant was considered a data point. We used the section divisions to assist in identifying collection species to maximize evolutionary relationships within the genus as a surrogate to an inferred phylogeny. We did not attempt to take host plant range into account, since there was substantial variation in species range and distribution among the host plant species.

### Study taxa

Leaf miners are herbivorous insects that live within and feed upon internal plant tissue, but do not induce the host to create additional plant tissue (Connor and Taverner 1997; Sinclair and Hughes 2008). Leaf miners generally have narrow host preferences, with the majority being restricted to one or two plant species (Fernandes et al. 2004; Hespenheide 1991; Lopez-Vaamonde et al. 2003; Memmott et al. 1994). Their often monophagous lifestyle, as in many other insect–host relationships, has been attributed to their adaptation to process only a certain set of plant chemicals (Schoonhoven et al. 2005). This "chemical" specificity ensures that host switches are uncommon, reinforcing the evolutionary relationships that exist between groups (Dethier 1952; Feeny 1975).

Insect galls are a reaction by plants to the mechanical effects of feeding, and the effect of insect saliva, which results in the proliferation of plant tissue. Galls may provide two major functions: refuge for the inducing insect from natural enemies and harsh abiotic factors, and access to readily available suitable food (Austin and Dangerfield 1998; Goncalves-Alvim and Fernandes 2001). Galls commonly have a characteristic morphology specific to the inducing insect, with each gall morph being widely accepted as belonging to a different galling species (Austin and Dangerfield 1998; Crespi et al. 1997; Cuevas-Reyes et al. 2003, 2004; Price et al. 1998). Gall-inducing insect species are commonly associated with one specific host plant (Abrahamson et al. 2003; Espirito-Santo and Fernandes 2007), and along with miners are considered the most specialised of all insect herbivores (Cuevas-Reyes et al. 2004; Gaston et al. 1992; Goncalves-Alvim and Fernandes 2001).

### Plant trait analysis

The following four plant traits were assessed on each of the 46 *Acacia* species: leaf/phyllode thickness, SLA, % phosphorus, and C:N ratio. The foliage properties measured follow Mooney and Gulmon (1982), Coley et al. (1985), Matson et al. (1994), Landsberg and Gillieson (1995) and Andrew and Hughes (2005b) to encompass a range of traits that are both sensitive to environmental constraints and differ measurably between plant species. The plants that these measurements were taken from were also used in the subsequent leaf miner and plant galler analyses.

Five fully expanded healthy leaves (using 10 pinnae per leaf) or phyllodes were removed from five individual plants of each species for further analyses. For brevity, we follow McDonald et al. (2003), and use the word "leaf" to refer to any green surface carrying out most of the plant's photosynthesis. In the field, the thickness of the foliage from the five leaves from five plants of each species were measured using digital calipers, and the foliage area was scanned using a flat bed scanner (with images saved digitally and labelled for further processing). Leaf surface area was then calculated from the scanned images using ImageJ® (Version 1.38x), and this area, along with the dry weights of the five measured leaves, was used to determine surface

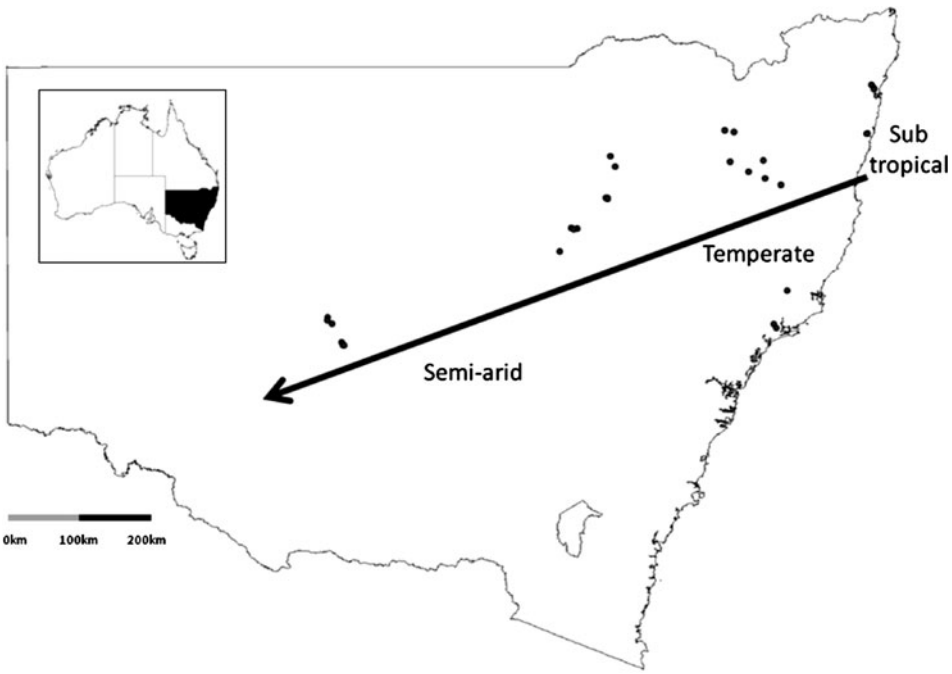


**Fig. 1** Map of study sites, NSW, Australia. The climatic gradient is represented by the *arrow* identifying the broad climate zones: semi-arid, temperate and subtropical. *Each point* represents one study site within the zone

leaf area (SLA = surface area ($cm^2$)/dry weight (g)). All foliage samples were then oven dried at 65°C for a period of 48 h. The dried foliage from each plant was then bulked, ground and sieved using a 0.5 mm aperture for chemical processing. Percentage phosphorus was measured following the methods outlined by Anderson and Henderson (1986). The carbon to nitrogen ratio for foliage was assessed using a Carlo Erba NA 1500 solid sample analyser coupled to a TracerMass stable isotope analyser. A single value was taken for each plant species per plant trait measured (an average for thickness and SLA and the single bulked value for %P and C:N ratio).

Other factors that are generally thought to influence insect species richness were not included in the scope of this study: host plant distribution, host plant phylogeny, and insect identity. Host plant patch size and distribution range is thought to have a positive effect on insect species richness (Cornell 1985; Strong et al. 1984), but this is not conclusive for endophagous insects (Fernandes and Price 1988). Blanche and Westoby (1996) did find a difference between species with large and small geographical ranges, but these differences were due more to greater species turnover between more widespread locations rather than higher local species richness. In this study we did not include host plant distribution as a variable since we assessed a host plant species endophagous community at one site. For it to be included as a variable, samples of endophagous insects would need to be collected for each host plant species at multiple sites throughout its distribution. Host plant phylogeny and endophagous insect identity may also have some influence on species richness patterns. That is, more closely related host plants may have more closely related insects feeding on them. This in itself is a substantial question relating to co-evolutionary relationships and parallel evolution (Bernays and Graham 1988). At this stage, neither the phylogeny of the *Acacia* nor the insect species identity (via rearing) have been verified. In fact, due to the lack of information on endophagous insects interacting with Australian *Acacia*, little if any ecological information is available at this stage. These are all fundamental questions that require further substantial information and detailed analyses in their own right.

## Leaf miner and plant galler assessment

Between 15 and 30 plants for each host plant species were randomly selected and assessed for leaf miners and insect gallers. Sampling of endophagous species stopped after 15 plants or before 30 plants if no new species were found on the last five plants surveyed (Table 1). A pilot survey we conducted determined that 30 plants per species maximized mining and galling species richness, and both groups generally reached an asymptote of no new species collected on a single host plant at an individual site after 30 plants (Cornell 1985). On small- to moderate-sized shrubs (<2 m), 100 random mature leaves/phyllodes were examined for the presence of mines, and all stems and foliage were examined for the presence of galls. Where tall shrubs or trees (>2 m) were sampled, only the areas within reach were examined and counted. When measuring endophagous species richness, it is widely accepted that each "morph" represents a different insect species (Austin and

**Table 1** Host plant species identity, site locations, plant-gall and leaf-miner species richness, number of plants sampled, and plant codes for all *Acacia* displayed in Fig. 2

| Section | Species | Area | Latitude | Longitude | Plant code | Number of plants sampled | Number of leaf-miner species collected | Number of plant-galler species collected |
|---|---|---|---|---|---|---|---|---|
| More subtropical | | | | | | | | |
| *Phyllodineae* | *suaveolens* | Bundjalung NP | 29°18.252S | 153°14.990E | 1 | 17 | 4 | 0 |
| *Plurinerves* | *baeuerlenii* | Bundjalung NP | 29°18.759S | 153°14.893E | 2 | 19 | 6 | 3 |
| *Phyllodineae* | *myrtifolia* | Bundjalung NP | 29°18.581S | 153°14.892E | 3 | 18 | 5 | 0 |
| *Juliflorae* | *concurrens* | Devils Pulpit SF | 29°15.117S | 153°12.939E | 4 | 30 | 12 | 3 |
| *Juliflorae* | *aulacocarpa* | Devils Pulpit SF | 29°15.117S | 153°12.939E | 5 | 30 | 10 | 3 |
| *Plurinerves* | *complanata* | Newfoundland SF | 29°56.327S | 153°09.609E | 6 | 30 | 7 | 5 |
| *Botrycephalae* | *terminalis* | Newfoundland SF | 29°56.327S | 153°09.609E | 7 | 16 | 1 | 2 |
| *Botrycephalae* | *oshanesii* | Newfoundland SF | 29°56.349S | 153°09 439E | 8 | 18 | 1 | 4 |
| *Botrycephalae* | *irrorata* | Newfoundland SF | 29°56.349S | 153°09.439E | 9 | 24 | 1 | 9 |
| *Phyllodineae* | *fimbriata* | Newfoundland SF | 29°56.349S | 153°09.439E | 10 | 20 | 0 | 7 |
| *Plurinerves* | *elongata* | Newfoundland SF | 29°56.546S | 153°08.920E | 11 | 23 | 3 | 1 |
| *Juliflorae* | *leiocalyx* | Newfoundland SF | 29°56.546S | 153°08.920E | 12 | 30 | 9 | 4 |
| *Juliflorae* | *floribunda* | The Glen NR | 32°10.019S | 152°01.467E | 13 | 30 | 6 | 2 |
| *Plurinerves* | *implexa* | The Glen NR | 32°10.019S | 152°01.467E | 14 | 30 | 9 | 5 |
| *Juliflorae* | *blakeii* | Oxley Wild Rivers NP | 30°39.976S | 151°56.040E | 15 | 30 | 7 | 1 |
| *Juliflorae* | *longifolia* | Medovue SCA | 32°41.772S | 151°52.287E | 16 | 30 | 10 | 4 |
| *Phyllodineae* | *falcata* | Wallaroo SF | 32°38.274S | 151°50.214E | 17 | 30 | 14 | 1 |
| *Botrycephalae* | *filicifolia* | Imbota NR | 30°34.589S | 151°42.695E | 18 | 30 | 0 | 12 |
| *Botrycephalae* | *dealbata* | Black Mountain | 30°19.293S | 151°41.332E | 19 | 21 | 0 | 8 |
| *Juliflorae* | *caroleae* | East Pilliga NR | 30°51.945S | 151°32.468E | 20 | 30 | 6 | 5 |
| *Phyllodineae* | *neriifolia* | Armidale-Bundarra Rd | 30°29.113S | 151°286.49E | 21 | 30 | 9 | 9 |
| *Plurinerves* | *viscidula* | Mt Topper SF | 29°55.152S | 151°16.153E | 22 | 16 | 0 | 1 |
| *Plurinerves* | *dawsonii* | Thunderbolts Way | 30°20.442S | 151°13.029E | 23 | 15 | 0 | 0 |
| *Phyllodineae* | *flexifolia* | Thunderbolts Way | 30°20.442S | 151°13.029E | 24 | 15 | 0 | 2 |
| *Botrycephalae* | *leucoclada* | Clive SF | 29°53.658S | 151°08.310E | 25 | 21 | 0 | 12 |
| *Plurinerves* | *harpophylla* | Brigalow Park NR | 30°24.645S | 149°35.313E | 26 | 30 | 3 | 12 |
| *Plurinerves* | *omalophylla* | East Pilliga NR | 30°15.760S | 149°31.236E | 27 | 30 | 3 | 5 |
| *Phyllodineae* | *pravifolia* | East Pilliga NR | 30°51.265S | 149°28.806E | 28 | 15 | 1 | 0 |
| *Botrycephalae* | *spectabilis* | East Pilliga NR | 30°51.265S | 149°28.806E | 29 | 30 | 4 | 2 |
| *Juliflorae* | *doratoxylon* | East Pilliga NR | 30°51.237S | 149°28.785E | 30 | 15 | 2 | 1 |
| *Phyllodineae* | *uncinata* | East Pilliga NR | 30°51.072S | 149°27.541E | 31 | 30 | 7 | 2 |
| *Botrycephalae* | *polybotrya* | East Pilliga NR | 30°51.072S | 149°27.541E | 32 | 30 | 1 | 8 |
| *Phyllodineae* | *dorothea* | Warrumbungle NP | 31°17.336S | 149°03.431E | 33 | 30 | 5 | 7 |
| *Botrycephalae* | *mearnsii* | Warrumbungle NP | 31°17.835S | 149°00.474E | 34 | 30 | 0 | 7 |
| *Juliflorae* | *cheelii* | Warrumbungle NP | 31°16.574S | 148°58.092E | 35 | 30 | 5 | 7 |
| *Plurinerves* | *montana* | Biddon NR | 31°36.756S | 148°48.410E | 36 | 18 | 3 | 2 |
| *Phyllodineae* | *tindaleae* | Nombinnie NR | 32°56.345S | 145°45.215E | 37 | 16 | 0 | 2 |
| *Plurinerves* | *wilhelmiana* | Nombinnie NR | 32°56.265S | 145°44.346E | 38 | 18 | 0 | 5 |
| *Juliflorae* | *triptera* | Nombinnie NR | 32°54.365S | 145°43.554E | 39 | 18 | 2 | 2 |
| *Phyllodineae* | *brachybotrya* | Nombinnie NR | 32°54.054S | 145°43.487E | 40 | 24 | 4 | 2 |
| *Juliflorae* | *burkittii* | Nombinnie NR | 32°53.986S | 145°43.467E | 41 | 15 | 0 | 1 |
| *Plurinerves* | *havilandiorum* | Nombinnie NR | 32°53.986S | 145°43.467E | 42 | 16 | 0 | 1 |
| *Botrycephalae* | *deanei* | Yathong NR | 32°38.022S | 145°35.414E | 43 | 18 | 0 | 14 |
| *Plurinerves* | *colletioides* | Yathong NR | 32°32.649S | 145°31.649E | 44 | 16 | 0 | 2 |
| *Phyllodineae* | *hakeoides* | Yathong NR | 32°32.649S | 145°31.649E | 45 | 19 | 5 | 0 |

**Table 1** continued

| Section | Species | Area | Latitude | Longitude | Plant code | Number of plants sampled | Number of leaf-miner species collected | Number of plant-galler species collected |
|---|---|---|---|---|---|---|---|---|
| More arid | | | | | | | | |
| *Juliflorae* | *aneura* | Yathong NR | 32°35.356S | 145°31.201E | 46 | 30 | 1 | 12 |

Dangerfield 1998; Crespi et al. 1997; Cuevas-Reyes et al. 2003, 2004; Hering 1951; Sinclair and Hughes 2008). Each new mine or gall was collected and assigned a morphotype number so that only new morphotypes were counted. All mine and gall morphotypes were photographed and catalogued for the 46 species of *Acacia* sampled.

### Data analysis

To determine how host plant species relationships varied according to plant traits and climate variables, a principal coordinates analysis (PCA) was performed on the "normalised" plant trait and climate data using PRIMER version 6.1.9 (Clarke and Gorley 2006). The first two PC axes together explained 61.9% of the variation (PC1 = 36.7%, PC2 = 25.2%) among the 46 *Acacia* species ("Electronic Supplementary Material" Table 1). Strong eigenvectors on PC1 included the following plant traits: foliage thickness, SLA, % phosphorus, C:N ratio; and the following climatic variables: mean annual rainfall and mean maximum temperature. Strong eigenvectors on PC2 included only one plant trait (C:N ratio) as well as the mean minimum temperature, mean annual rainfall, and latitude.

To assess the adequacy of the sampling of leaf miners and plant gallers (Andrew and Hughes 2005a), Coleman and Chao-1 curves were generated using EstimateS 8.0.0 (Colwell 2006). Galling and mining datasets were assessed separately due to the different methods of collection.

Model selection based on Akaike's information criterion (AIC) was used to assess the most important variables that explain mining and galler diversity using Spatial Analysis in Macroecology (SAM) (Rangel et al. 2006). SAM gives an output showing every model generated. The log-likelihood, L(gilx), of each ordinary least squares regression model reflects the overall fit of that model; a value of 1 indicates the best fit, while decreasing fitness is represented by smaller values. The delta AICc is a measure of each model relative to the best model, which is given a value of zero (Mazerolle 2006). Models with a delta AICc of <2 were considered in our analysis (see Rangel et al. 2006). Akaike weights were also used to measure the relative importance of each explanatory variable; the weights of all models in which each variable was present were summed and this was then compared to the sum of the weights of all of the models that did not include the variable (Mazerolle 2006) and was automatically generated during analyses. The four plant trait variables used in the PCA (% phosphorus, SLA, C:N ratio and leaf/phyllode thickness), climatic variables (mean maximum temperature, mean minimum temperature, mean annual rainfall), and latitude were used as response variables. Climatic variables were generated for each site using ANUCLIM 5.1 (Houlder et al. 2000).

To assess which environmental variables had the strongest correlation with galler and miner community structure (based on presence/absence), a canonical analysis of principal coordinates (CAP) was carried out using PERMANOVA+ for Primer (Anderson et al. 2008). CAP also determines the number of optimal canonical axes (*m*) that best explain the variation of the data. Only the first two CAP axes will be assessed in detail. The four plant trait variables used (% phosphorus, SLA, C:N ratio and foliage thickness), as well as the climatic variables (mean maximum temperature, mean minimum temperature, mean annual rainfall), and the latitude were used as response variables. Climatic variables were generated from each site using ANUCLIM 5.1 (Houlder et al. 2000).

## Results

### Leaf miner and plant gall species richness

In total, 97 leaf-mining species were collected (Table 1). *Acacia falcata* (sampled from a temperate site) supported the most leaf miner species (14), followed by 12 leaf miner species on *A. concurrens* (subtropical site), and 10 species on each of *A. aulacocarpa* (subtropical site) and *A. longifolia* (temperate site). The Chao-1 species estimation index predicted that there are potentially 110 species within the community, across all climatic zones and host plant species, indicating that 88% of the mining population was sampled.

Eighty-four plant-galling species were collected (Table 1). The highest galler richness (14 species) was found on *A. deanii*, the only bipinnate species from the more arid areas, followed by 12 galling species on each of

*A. aneura* (also from the more arid areas), *A. harpophylla*, *A. leucoclada*, and *A. filicifolia* (all from the temperate areas). The Chao-1 species estimation index predicts that there are potentially 103 species within the community, across all climatic zones and *Acacia* sections, indicating that 82% of the galling population was sampled.

To assess which plant traits and climatic variables best explain species richness patterns, the AIC model selection technique was used ("Electronic Supplementary Material" Table 2). The most important factors explaining leaf miner richness along the climatic gradient included SLA (this factor was present in all 15 models assessed), and both mean annual rainfall and foliage thickness (both present in 13 models). The model with the largest $r^2$ value for explaining foliage miner species richness included the following factors: mean annual rainfall, latitude, leaf thickness and SLA ($r^2 = 0.341$; "Electronic Supplementary Material" Table 2). The most important factor explaining plant galler richness across the climatic gradient was the C:N ratio, which was present in 11 of the 14 models (all other factors were present in ≤5 models). The model with the largest $r^2$ value for plant galler richness included the following factors: mean annual rainfall, latitude, C:N ratio, and SLA ($r^2 = 0.228$; "Electronic Supplementary Material" Table 2).

### Assemblage structure

Canonical analysis of the principal coordinates (CAP) for the leaf miner and plant galler community compositions produced substantially different results (Fig. 2a, b; "Electronic Supplementary Material" Table 3). For miners, the CAP analysis recognized eight PCO axes (*m*) that encapsulated 63% of the total variability (Fig. 2a). The first squared canonical correlation explained 79% of the variation, whilst the second canonical correlation explained 59% of the variation. The only variables to exhibit strong correlations with CAP axis 1 were mean annual rainfall (0.64), SLA (0.371), and foliage thickness (0.3). The variables that showed strong correlations with CAP axis 2 included SLA (0.55), foliage thickness (0.49), minimum mean temperature (0.47), and mean annual rainfall (0.4). Mining community structure tended to be more strongly related to mean annual rainfall and C:N ratio.

For gallers, the CAP analysis recognized seven PCO axes (*m*) which encapsulated 70% of the total variability (Fig. 2b; "Electronic Supplementary Material" Table 3). The first squared canonical correlation explained 65% of the variation, whilst the second canonical correlation explained 60% of the variation. The variables that exhibited strong correlations with CAP axis 1 included C:N ratio (−0.52), %P (0.49), latitude (0.43), and mean minimum temperature (0.4). The variables that showed strong correlations with CAP axis 2 included foliage thickness (0.62) and mean annual rainfall (−0.49).

## Discussion

While several studies have examined the importance of climate, host plant phylogeny, and host plant traits in influencing insect assemblage structure (Hairston et al. 1960; Hodkinson et al. 1999; Novotny et al. 2002; Speight et al. 1999), the relative influences of two or more factors remain poorly understood. Here, using highly specialized herbivores (plant gallers and leaf miners) to assess the influences of these factors, we found that the factors that best explained leaf miner richness across the climatic gradient included specific leaf area (SLA), foliage thickness and mean annual rainfall, whereas C:N ratio was the most important factor that explained plant galler richness across the climatic gradient. Leaf miner assemblage structure was most influenced by SLA, foliage thickness, mean minimum temperature and mean annual rainfall, whilst plant galler assemblages were influenced by C:N ratio, %P, foliage thickness, mean minimum temperature and mean annual rainfall.

This study assessed endophagous insect species richness and composition patterns along a 950 km environmental gradient and across 46 host plant species from the genus *Acacia*. Mean annual rainfall across the gradient ranged between 365.0 and 1,451.9 mm (BOM 2008). Average maximum annual temperature ranged between 19.5 and 25.2°C (BOM 2008). Although it was a snapshot study, we did use consistent methods on host plant species that were abundant at each site. Other studies assessing large-scale changes have used a range of host plant species and continents (Price et al. 1998), and along rainfall gradients in tropical Australia (Blanche 2000) and eastern Australia (Sinclair and Hughes 2008). However, no previous studies have assessed the influences of a range of biotic and abiotic variables on the species richness patterns of both major endophagous taxa across such an extensive gradient.

Climatic variables, particularly mean maximum temperature, had a substantial influence on the plant traits measured. Average foliage thickness increased with environmental harshness (as indicated in this study by the close correlation with mean annual temperature), while SLA and percentage P decreased. As sclerophyllous species are frequently associated with harsh environments (Fernandes and Price 1991; Turner 1994), and typically produce foliage of increased thickness and reduced surface area (Medina et al. 1990; Turner 1994), this trend can most probably be attributed to increased levels of sclerophylly at the arid and semi-arid sites. Mean maximum temperature had a negative influence on foliage SLA. Previous studies

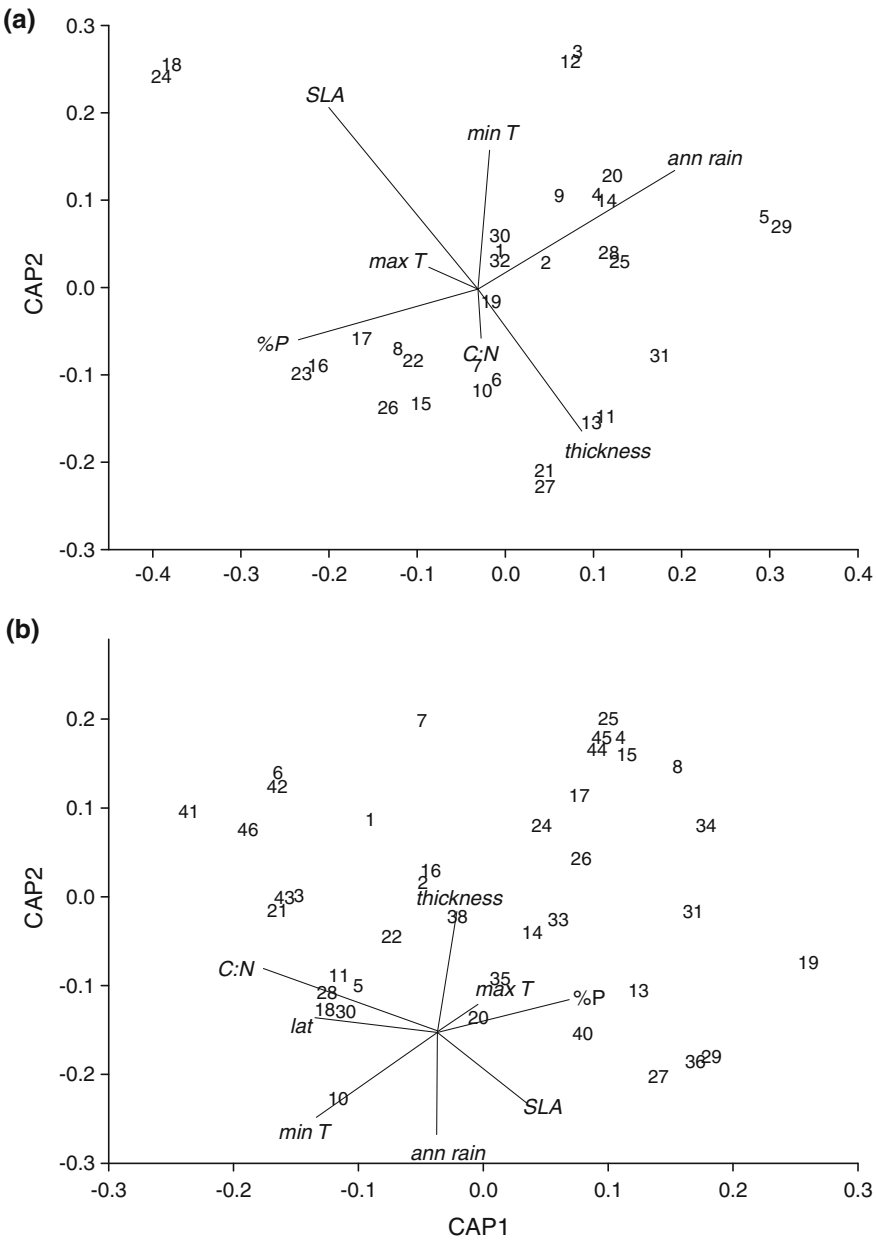


**Fig. 2** Canonical analysis of principal coordinates (CAP) for **a** leaf miners and **b** plant gallers (based on the presence/absence of gall species using Bray–Curtis similarity). Variables used included plant traits (SLA, % phosphorus, C:N ratio, foliage thickness), climatic variables (mean minimum temperature, mean maximum temperature, and mean annual rainfall), and latitude. Plant species codes are outlined in Table 1

have emphasised the impact of climate on SLA, with the majority claiming an increase in SLA with climatic favourability (Landsberg and Gillieson 1995; Medina et al. 1990; Mooney et al. 1978). Specific leaf area in this study varied substantially due to the unique form of the *Botrycephalae* bipinnate leaf in comparison to the single-bladed phyllodes presented in the other three sections. Mean maximum temperature also had a significant influence over % phosphorus levels. The more arid species exhibited lower levels of phosphorus compared to the more mesic host plants. This finding is in line with previous studies which found that plant species show higher phosphorus levels in the more temperate east then in the arid west of the continent (Majer et al. 1992).

Leaf miner species richness was strongly influenced by climate variables (mean annual rainfall) and plant traits (SLA and foliage thickness). As expected, miner richness was lower in arid habitats and increased with climatic favourability (Andrew and Hughes 2005b; Fernandes et al. 2004; Sinclair and Hughes 2008). Apart from the impact of desiccation, climate may influence species diversity through its impacts on specific plant traits: SLA and leaf thickness are physical foliage traits that correlated with miner diversity in this study. The trends observed here may be due to increased levels of sclerophylly in harsh environments. Sclerophylly has long been demonstrated to influence the species diversities of endophagous communities (Lara et al. 2002). Sclerophylly is frequently

associated with harsh environments (Fernandes et al. 2004; Fernandes and Price 1991, 1992; Medina et al. 1990; Orians and Milewski 2007; Turner 1994), and sclerophyllous plants are known to have higher levels of secondary compounds, and smaller, thicker leaves (Hartley and Jones 1997; Medina et al. 1990; Turner 1994). These features have been shown to impact upon mining communities. Secondary compounds reduce fitness (Scriber 1977), and miners preferentially select larger leaves (Faeth et al. 1981b). High-temperature and low-rainfall habitats, with their associated plant traits, are largely inappropriate for leaf mining communities, structuring their distributions and ultimately determining levels of species richness.

Climate may also impact on mining richness via its effects on general plant venation. *Acacia* species which have veins that are numerous, parallel, close together and lack anastomoses are more abundant in semi-arid and arid areas than in mesic, while *Acacia* species with a few, distant, longitudinal veins with or without anastomoses tend to predominate in the tropical and subtropical north of the continent and along parts of the great dividing range (Hnatiuk and Maslin 1988). Miners will preferentially select leaves and phyllodes with reduced venation (Hespenheide 1991). This preference results in an increase in richness in habitats supporting plants of reduced venation; that is, tropical and temperate environments—a trend observed in our results. Miner richness were also low on *Botrycephalae* host plants due to a number of morphological features associated with this section—primarily bipinnate foliage in the adult form. As miners are shown to preferentially select leaves of increasing surface area (Faeth et al. 1981b; Whitham 1980), and survival levels are dependent on oviposition accuracy, which increases with target size (Ferrier and Price 2004), this feature of *Botrycephalae* may severely limit levels of species richness. Plant traits were shown to have some influence on leaf miner species richness. The traits of highest significance for mining species richness were foliage SLA (a factor in all AIC models), and, for mining communities, SLA and foliage thickness (CAP axis 1 and 2). This supports the idea that miners preferentially select foliage that is structurally appropriate and less sclerophyllous (Sinclair and Hughes 2008).

Although some studies have claimed that the galling lifestyle is an adaptation to harsh environmental conditions (Price et al. 1987), no general trend supporting this hypothesis was found for *Acacia* gallers. We found that none of the climatic variables strongly influenced plant gall species richness, in line with the results of other studies, which did not support the idea that arid environments in Australia contain more galling insect species than cooler, wetter habitats (Blanche 2000; Blanche and Westoby 1995, 1996). Rather, other environmental factors, such as plant chemistry (C:N ratio in this study) or sclerophylly and vegetation composition appear to be more important determinants in other studies (Goncalves-Alvim and Fernandes 2001; Veldtman and McGeoch 2003). The venation of the species in the section *Phyllodineae* may impact on galler richness. The section *Phyllodineae* presents univeined phyllodes, in contrast to the multiveined phyllodes exhibited by species of the *Juliflorae* and *Plurinerves* (Maslin 2004; Matson et al. 1994). Studies on Thysanoptera gallers suggest that the structure of the univeined phyllode may be more difficult to manipulate than that of a multiveined phyllode (Crespi et al. 2004); the lower galler richness observed in species within the section *Phyllodineae* could therefore result from a physical barrier.

Foliage thickness may affect galling assemblages via its association with sclerophylly, as sclerophyllous foliage is generally relatively thick and has a low specific leaf area (Medina et al. 1990; Turner 1994), and gallers are known to present higher richness on scleromorphic vegetation (Fernandes and Price 1992; Wright and Samways 1998). In this study, SLA and foliage thickness had the strongest correlation with the second canonical axis explaining the variation in galling communities.

Plant traits are well known to be important factors in the determination of insect distribution and diversity. For miners, SLA and foliage thickness are of particular importance for explaining the variations observed in mining communities. Past studies have shown a general relationship between SLA and level of sclerophylly, with sclerophyllous plants usually producing foliage of reduced SLA (Medina et al. 1990). Other features of sclerophyllous foliage include small surface areas and high thickness (Turner 1994). As miners are shown to preferentially select foliage of increasing nutritional value, surface area and SLA (Faeth et al. 1981b; Whitham 1980), and survival levels are dependent on oviposition accuracy, which increases with target size (Ferrier and Price 2004), the features of sclerophyllous plants are not conducive to the development of large miner populations. As such, the highest mining levels are found in habitats with low levels of sclerophylly, larger SLAs and surface areas, and smaller average foliage thickness.

These results have important implications for our ability to predict the impacts of climate change over the coming century. Since 1950, the climate in the study region has experienced an increase in temperature and a decrease in precipitation (CSIRO 2007). Climatic predictions for the next 50 years show warming but also unpredictable changes in rainfall (CSIRO 2007). Species most at risk from climate change include those with narrow physiological tolerances, poor dispersal capabilities and narrow geographic ranges (Steffen et al. 2009). Patterns of species richness and assemblage structure are influenced by a range

of large-scale traits, including climate and host plant physical and chemical traits. If climate change exerts both warming and drying effects, or at least results in more variable rainfall patterns, we may then expect plant foliage to become tougher and thicker, and to exhibit changes in chemical composition (in particular a higher C:N ratio). In turn, we would expect both plant-galler and leaf-miner assemblages to respond to these changes via a substantial shift in the assemblages that the host plant may harbor. To test this further, life history, physiological and behavioural adaptations of the species need to be assessed.

This is the first study we know of that has assessed the relative influences that climate and host plant traits have on endophagous diversity across a broad environmental gradient and a suite of widely distributed and morphologically variable host genera. Within this study, a range of climatic and/or plant traits play a role in structuring the patterns of leaf-miner and plant galler assemblages. For miners, the plant traits of SLA and foliage thickness and the climatic traits of mean minimum temperature and mean annual rainfall were important in structuring assemblages. For gallers, plant traits such as SLA, C:N ratio, %P and foliage thickness, and climatic traits such as mean minimum temperature and mean annual rainfall were important in structuring communities. Such methods provide key insights into endophage diversity and provide a solid basis for assessing their responses to a changing climate.

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